

A PHYLOGENETIC HYPOTHESIS FOR THE GOLDENASTERS
(ASTERACEAE: ASTEREAЕ)

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ABSTRACT

The seven genera of the goldenaster lineage are included in a phylogenetic analysis based primarily on morphological data. They are hypothesized to form three separate clades: (1) *Chrysopsis* (including *Bradburia*), *Osbertia*, and *Noticastrum*, (2) *Croptilon* and *Pityopsis*, which are sister genera, and *To mentaurum*, and (3) *Heterotheca* (including sects. *Ammodia*, *Heterotheca*, and *Phyllothe ca*). The genus most closely related to the goldenaster lineage is taken to be *Ionactis* (= *Aster* sect. *Ianthe*).

KEY WORDS: *Heterotheca*, *Ionactis*, *Aster*, Asteraceae, Astereae

Recent studies of restriction site variation in chloroplast DNA of North American Astereae (Suh 1989; Morgan 1990) have produced a relatively clear delimitation of a phylogenetically coherent group of genera termed the "goldenasters." Suh's sample included *Croptilon* Rafin., *Pityopsis* Nutt., *Heterotheca* Cass. (sect. *Heterotheca*), *Bradburia* Torr. & Gray, and *Chrysopsis* (Nutt.) Ell.; Morgan's sample included *Croptilon* and *Osbertia* E. Greene. Semple *et al.* (1980) postulated that *Chrysopsis* and *Bradburia* are part of an evolutionary lineage completely apart from the others, but for the most part, recent treatments have recognized the goldenaster genera as a natural group, at least implicitly, since many authors have viewed *Chrysopsis*, *Pityopsis*, and *Heterotheca* (including sects. *Heterotheca*, *Phyllothe ca* [Nutt.] Harms, and *Ammodia* [Nutt.] Harms) in various combinations as only one or two genera (see Semple 1977 for a review). The studies of Semple and colleagues have been instrumental in illuminating the distinctions among these taxa (see Semple *et al.* 1980 for a review and overview) and have provided separate taxonomic studies of *Chrysopsis* (Semple 1981), *Pityopsis* (Semple & Bowers 1985), *Heterotheca* sect. *Ammodia* (Semple 1988), and *Bradburia* (Semple & Chinnappa 1984). Other of the genera have also been the subjects of relatively recent taxonomic

treatments (*Croptilon*, Smith 1966, 1981; *Osbertia*, Turner & Sundberg 1986, Nesom 1991a; *Heterotheca* sect. *Heterotheca*, Nesom 1990), and Nesom (1991c) has presented evidence for uniting the monotypic *Bradburia* with *Chrysopsis* in a phylogenetic analysis of the latter.

In addition to the genera above, Turner & Sundberg (1986) noted that the South American genus *Noticastrum* DC. (see Cuatrecasas 1973; Zardini 1978) probably should be included as a member of the goldenaster lineage, and evidence from the present study supports its inclusion. *Tomentaurum* Nesom, a newly described monotypic genus from western Mexico has been added to the goldenasters (Nesom 1991b).

There is further indication, based on the cpDNA studies of Suh (1989) and Morgan (1990), that the white rayed *Boltonia* L'Herit. and *Chloracantha* Nesom *et al.* are more closely related to the goldenasters than to any other species in their studies, although they are highly divergent in morphology and appear to be weakly associated somewhere at the very base of the phylad (Nesom *et al.* 1991). They are not included in the present analysis.

The molecular studies of Suh & Morgan placed the goldenaster lineage most closely to the *Machaeranthera* Nees and *Aster* L. lineages (see Nesom *et al.* 1989, for a summary). Neither of their studies, however, included a wide range of species traditionally accommodated in *Aster*. A morphologically based phylogenetic overview of *Aster* and related genera (Nesom in prep.) hypothesizes that the taxa most similar to the goldenasters lie among the groups of *Aster* not included in the recent molecular analyses, those with carinate phyllaries, a double pappus, and a base chromosome number of $x = 9$. Among these, *Aster* subg. *Ianthe* [Torr. & Gray] A. Gray, with strongly asymmetric carpodia, is hypothesized to be the sister group to the goldenasters. Additional comments are provided by Nesom & Leary (submitted), who treat the group at generic rank as *Ionactis* E. Greene and add a fourth species to it.

The studies noted above have offered various ideas regarding relationships of genera within the goldenaster group, but none have included all of the taxa involved. The present study confirms the evolutionary unity of the seven genera of goldenasters on a morphological basis and provides a phylogenetic hypothesis for all of them.

CLADISTIC ANALYSIS - METHODS

Studies of microcharacters were made with a compound microscope. Glands, trichomes, foliar veins were studied from epidermal "skims" and cross sections made with a razor from stems and leaves; these and dissected flowers have been mounted on slides in Hoyer's Medium. A list of specimens from which slides have been made is deposited at TEX; all voucher specimens are deposited in TEX. Characters and character states used in the analysis are given in Table

1; coding for the individual taxa are in Table 2; discussion of variability in the characters is provided in the Appendix. The data were analyzed using PAUP (Swofford 1985) with Wagner parsimony.

Some decisions regarding evolutionarily primitive character states in *Chrysopsis*, which comprises two sharply disparate sections, have been made in a separate analysis (Nesom 1991c). Section *Phyllothea* of *Heterotheca* is a variable group and is represented in the present analysis by two species, *H. mexicana* Harms ex B. Turner and *H. stenophylla* (A. Gray) Shinnery, these chosen to broaden the variability included in the character scoring. The genus *Ionactis* serves as the outgroup in the present analysis, since it appears to be the group most closely similar and probably most closely related to the goldenasters.

RESULTS and DISCUSSION

The goldenaster lineage is characterized by a number of morphological features, some shared with related groups and some that distinguish it from the *Aster* and *Machaeranthera* lineages: stipitate glandular herbage, carinate phyllaries, yellow ray flowers, throat tissues of disc corollas with numerous, straight sided, elongate crystals, disc style branches have linear-lanceolate appendages, multinerved achenes, asymmetric carpodia, and pappus of slender, basally terete bristles with a much shorter outer series. In *Heterotheca* and *Chrysopsis*, the heads are borne in a corymboid cyme arising from the distal portion of the main branches, with a tendency to be somewhat more loosely arranged in *Pityopsis* and *Croptilon*. Further, it seems clear that the base chromosome number for the group is $x = 9$. Of particular significance in this study has been the discovery that the goldenaster genera appear to stand apart from almost all other North American Astereae in their production of long, straight sided crystals in the tissues of the disc corolla throats. Similar crystals have been observed elsewhere only in *Xylorhiza* Nutt., *Grindelia* Willd., and *Prionopsis* Nutt. (Nesom *et al.* submitted), which are related to *Machaeranthera* rather than the goldenasters (Morgan 1990). Further details regarding these crystals are provided in the Appendix.

A single tree of 36 steps (Fig. 1) accounts for the distribution of character states scored in the present analysis. Three primary lineages are defined, referred to here as the *Chrysopsis*, *Heterotheca*, and *Pityopsis* lineages, since the present study fully corroborates the earlier conclusion by Semple *et al.* (1980) that each of these three genera is phylogenetically distinct from the other two. The single character (no. 18, vestiture of the disc corolla lobes) that unites the *Heterotheca* and *Pityopsis* lineages is the most homoplasious of all those in the present study, and it must be viewed as nearly weightless evidence in resolving what otherwise would be a basal trichotomy. If it were assumed

TABLE 1. Characters and character states.

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1. Chromosome number, (0) $x = 9$ or 7 (1) $x = 5$ or 4
 2. Taproot or rhizomes, (0) rhizomes (1) taproot
 3. Leaf shape and venation pattern, (0) obovate to oblanceolate, net veined (1) linear, parallel veined or with a strong tendency for parallel veins
 4. Leaf venation/anatomy, (0) veins not strongly sclerenchymatous, not raised above the lamina (1) veins with associated massive sclerenchyma, prominently superficial and forming ridges,
 5. Biseriate (Type C) trichomes, (0) without a differentiated head or the head merely 2 celled, the only form of Type C trichomes present (1) at least some with a highly elaborated head 4-8 cells wide at the apex, on a distinct stalk
 6. Type A trichomes on herbage, (0) abundant (1) few in number or completely absent
 7. Type A trichomes, (0) thick-walled, terete, or absent (1) thin walled, often flattened and twisted
 8. Type A trichomes - outer walls, (0) smooth or absent (1) papillate
 9. Type B trichomes, (0) minute, less than 0.5 mm long (1) filamentous, highly elaborated in length, sometimes forming a dense, close, tomentum
 10. Head arrangement, (0) numerous in a corymboid cyme arising from branches on the upper third of the primary stem (1) solitary on monocephalous stems
 11. Head width, (0) mostly (8-)10-20 mm (1) mostly 4-7 mm
 12. Phyllary morphology, (0) indurated at least basally, with a narrow, raised, white indurated keel (1) herbaceous throughout, or at least the medial nerve not at all keeled
 13. Ray corolla color, (0) bluish (1) yellow
 14. Ray corolla color, (0) bluish or yellow (1) yellow, tinged with reddish purple
 15. Ray corolla behavior after stigma receptivity, (0) coiling (1) remaining straight

TABLE 1. (continued).

16. Cells of disc corolla throat, (0) with stellate "sand" crystals or without crystals (1) with elongate, straight sided crystals
 17. Radial wall of cells of disc corolla throat, (0) broadly sinuate (1) straight
 18. Disc corolla lobes, vestiture (0) glabrous or with biseriate, glandular hairs (1) with uniseriate, acicular hairs, commonly also with obscure glandular hairs
 19. Vascular bundles in collecting appendages of disc flower style branches, (0) unsclerified (1) sclerified
 20. Disc achene surface, (0) with nerves subepidermal or raised but not resinous (1) with numerous, thin, slightly resinous nerves flush with surface
 21. Disc achene surface, (0) with (2-)8-26 thin, superficial, nerves, or the nerves not thick and rounded (1) with thick, rounded ridges, the nerves completely below the epidermal surface
 22. Disc achene nervation, (0) (6-)8-26 nerved (1) 2-(3-6) nerved
 23. Achene shape, side view, (0) narrowly oblong to oblong elliptic, symmetric (1) obovate, asymmetric
 24. Disc achene shape, (0) distinctly compressed (1) terete or subterete
 25. Pappus series, (0) double, the outer much shorter than the inner and varying from setae to linear scales (1) single, of bristles relatively even in length
 26. Pappus bristle shape in cross section, (0) terete (1) flattened
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TABLE 2. Data matrix for the goldenaster taxa analyzed.

Taxa	Character State					
<i>Ionactis</i> (IONACT)	00000	00000	00000	00000	00000	0
Sect. <i>Ammodia</i> (AMMODI)	01001	00100	00100	11110	01000	1
<i>Heterotheca mezicana</i> (HMEXIC)	01001	00100	00100	11111	01000	1
Sect. <i>Heterotheca</i> (HETERO)	01001	00100	00100	11011	01100	1
<i>Heterotheca stenophylla</i> (HSTENO)	01001	00100	00100	11011	01000	1
<i>Tomentaurum</i> (TOMENT)	?0001	10011	00100	11110	01000	0
<i>Pityopsis</i> (PITYOP)	00111	10010	10100	11110	01010	0
<i>Croptilon</i> (CROPTI)	01111	10010	10100	11010	01011	0
<i>Noticastrum</i> (NOTICA)	0?001	01001	00111	11110	01000	0
<i>Osbertia</i> (OSBERT)	10001	01001	01111	10010	01011	0
<i>Chrysopsis</i> (CHRYSO)	10001	01000	00100	11010	11100	0

that the Type A trichomes were present in the goldenaster ancestor and lost twice in the *Chrysopsis* lineage, the trichotomy would remain unresolved with the addition of a single additional step in the same character.

Each of the three goldenaster lineages is distinguished primarily by the nature of its vestiture (see Nesom 1976 and further comments in the Appendix). All of the goldenaster taxa usually have stipitate glandular hairs, but those of the *Chrysopsis* lineage are characterized by their relatively long Type A trichomes with thin, smooth walls, those of the *Heterotheca* lineage by Type A trichomes with papillate outer walls, and those of the *Pityopsis* lineage by the absence or near absence of Type A trichomes and the presence instead of greatly lengthened and prominent Type B trichomes.

Apart from the relationship of the three primary lineages, the goldenaster phylogeny appears to be relatively well resolved, based on the data available, but several other problematic and unsatisfying points remain. First, the placement of *Osbertia* and *Chrysopsis* as sister species, rather than *Osbertia* and *Noticastrum*, would be more consistent with a well known geographic pattern of diversification, where closely related taxa occur both in the southwestern United States and in eastern Mexico, and it would not require a parallel reduction in chromosome number from $x = 9$ to $x = 5$. A study of the $x = 5$ *Chrysopsis* and $x = 5$ *Osbertia* karyotypes might prove to be critical in this interpretation. Second, *Tomentaurum* is so very different from *Pityopsis* and *Croptilon* in habit, leaf morphology, and other features, as well as different from the probable ancestor to the whole goldenaster phylad, that it would not be surprising if it were placed, on the basis of additional evidence, closer to any of the other genera. Finally, *Heterotheca* (sensu Semple *et al.* 1980 and the

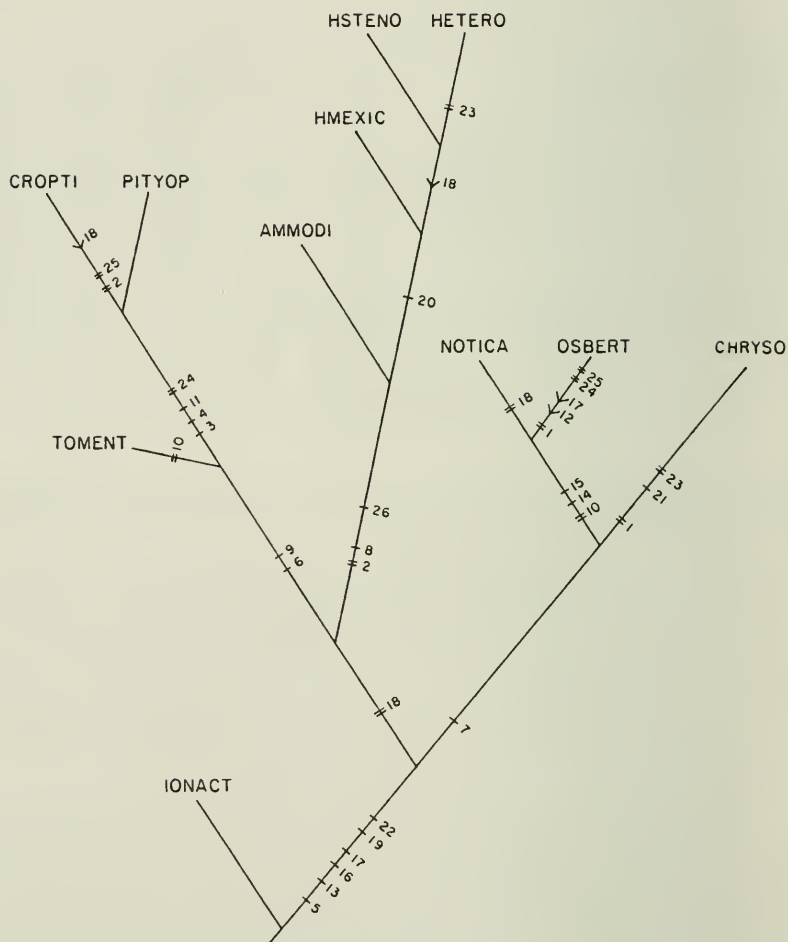


Figure 1. Phylogenetic reconstruction of the goldenaster lineage. Abbreviations for the taxa follow those in Table 2. Single slash = apomorphy or autapomorphy; double slash = parallelism; downward arrow = reversal.

present analysis) can be maintained as a single genus, but sect. *Phyllothea* probably is paraphyletic and better treated as several separate sections (the data of this analysis do not show this as clearly as possible). Alternatively, the monotypic *Heterothea* sect. *Ammodia* (*H. oregona* [Nutt.] Shinnery) might justifiably be segregated as a monotypic genus, as did Nuttall originally.

The cladistic topology postulated here, based on morphology, differs slightly from a relatively unresolved cladogram based on molecular data (Suh 1989), although the latter analysis included only four of the taxa treated here. Suh positioned *Heterothea* sect. *Heterothea*, *Pityopsis*, and *Croptilon* as a trichotomy that is phyletically coordinate with the species pair *Chrysopsis pilosa* Nutt. and *C. tezana* Nesom (= *Bradburia*). Both of the latter two are treated by Nesom (1991c) as *Chrysopsis* sect. *Bradburia* (Torr. & Gray) Nesom. Morgan's analysis (1990) included only two goldenaster genera and placed *Osbertia* coordinate with several species of *Croptilon*.

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LITERATURE CITED

- Carlquist, S. 1961. *Comparative Plant Anatomy*. Holt, Rinehart, & Winston, New York.
- Cuatrecasas, J. 1973. Miscellaneous notes on Neotropical Flora, III. *Phytologia* 25:249-256.
- Drury, D.G. & L. Watson. 1966. Taxonomic implications of a comparative anatomical study of Inuloideae-Compositae. *Amer. J. Bot.* 53:828-833.
- Hartman, R.L. 1990. A conspectus of *Machaeranthera* (Asteraceae: Asteraceae). *Phytologia* 68:439-465.
- Jones, A.G. 1980. A classification of the New World species of *Aster* (Asteraceae). *Brittonia* 32:230-239.
- Jones, A.G. & D. Young. 1983. Generic concepts of *Aster* (Asteraceae): A comparison of cladistic, phenetic, and cytological approaches. *Syst. Bot.* 8:71-84.

- Morgan, D.R. 1990. A systematic study of *Machaeranthera* (Asteraceae) and related groups using restriction analysis of chloroplast DNA and a taxonomic revision of *Machaeranthera* section *Psilactis*. Ph.D. dissertation, University of Texas, Austin.
- Nesom, G.L. 1976. A new species of *Erigeron* (Asteraceae) and its relatives in southwestern Utah. *Brittonia* 28:263-272.
- . 1989. Infrageneric taxonomy of New World *Erigeron* (Compositae: Astereae). *Phytologia* 67:67-93.
- . 1990. Taxonomy of *Heterotheca* sect. *Heterotheca* (Asteraceae: Astereae) in México, with comments on the taxa of the United States. *Phytologia* 69:282-294.
- . 1991a. Transfer of *Heterotheca bartlettii* to *Osbertia* (Asteraceae: Astereae). *Phytologia* 71:132-135.
- . 1991b. *Tomentaurum* (Asteraceae: Astereae), a new genus of goldenaster from Mexico. *Phytologia* 71:128-131.
- . 1991c. Union of *Bradburia* with *Chrysopsis* (Asteraceae: Astereae), with a phylogenetic hypothesis for *Chrysopsis*. *Phytologia* 71:109-121.
- . 1991d. Transfer of *Aster kingii* to *Tonestus* (Asteraceae: Astereae). *Phytologia* 71:122-127.
- . In prep. An overview of the phylogeny of *Aster* sensu lato (Asteraceae: Astereae).
- Nesom, G.L. & D.R. Morgan. 1990. Reinstatement of *Tonestus* (Astereae: Asteraceae). *Phytologia* 68:174-180.
- Nesom, G.L., Y. Suh, D.R. Morgan, & B.B. Simpson. 1989. *Xylothamia* (Astereae: Asteraceae), a new genus related to *Euthamia*. *Sida* 14:101-116.
- Nesom, G.L., Y. Suh, & B.B. Simpson. Submitted. The phylogenetic position of *Stephanodoria* (Asteraceae: Astereae). *Brittonia*
- Nesom, G.L., Y. Suh, D.R. Morgan, S.D. Sundberg, & B.B. Simpson. 1991. *Chloracantha*, a new genus of North American Astereae (Asteraceae). *Phytologia* 70:371-381.
- Nesom, G.L. & P.J. Leary. Submitted. A new species of *Ionactis* (Asteraceae: Astereae) from southern Nevada. *Brittonia*.

- Semple, J.C. 1977. Cytotaxonomy of *Chrysopsis* and *Heterotheca* (Compositae-Astereae): a new interpretation of phylogeny. *Canad. J. Bot.* 55:2503-2513.
- . 1981. A revision of the goldenaster genus *Chrysopsis* (Nutt.) Ell. nom. cons. (Compositae-Astereae). *Rhodora* 83:323-384.
- . 1984. Observations on the cytology, morphology, and ecology of *Bradburia hirtella* (Compositae-Astereae). *Syst. Bot.* 9:95-101.
- . 1988. *Heterotheca* sect. *Ammodia* (Compositae: Astereae): A multivariate study of *H. oregona* and specimens of Brewer's (golden)aster. *Syst. Bot.* 13:547-558.
- Semple, J.C., V.C. Blok, & P. Heiman. 1980. Morphological, anatomical, habit, and habitat differences among the goldenaster genera *Chrysopsis*, *Heterotheca*, and *Pityopsis* (Compositae-Astereae). *Canad. J. Bot.* 58:147-163.
- Semple, J.C. & F.D. Bowers. 1985. A revision of the goldenaster genus *Pityopsis* Nutt. (Compositae: Astereae). *Univ. Waterloo Biol. Ser.* 29:1-34.
- Semple, J.C. & C.C. Chinnappa. 1980. Karyotype evolution and chromosome numbers in *Chrysopsis* (Nutt.) Ell. sensu Semple (Compositae-Astereae). *Canad. J. Bot.* 58:164-171.
- Smith, E.B. 1966. Cytogenetics and phylogeny of *Haplopappus* section *Isopappus* (Compositae). *Canad. J. Genet. Cytol.* 8:14-36.
- . 1981. New combinations in *Croptilon* (Compositae-Astereae). *Sida* 9:59-63.
- Stirton, C.H. 1983. Nocturnal petal movements in the Asteraceae. *Bothalia* 14:1003-1006.
- Suh, Y. 1989. Phylogenetic studies of North American Astereae (Asteraceae) based on chloroplast DNA. Ph.D. dissertation, University of Texas, Austin.
- Swofford, D.L. 1985. PAUP: Phylogenetic analysis using parsimony, Vers. 2.4. Illinois Nat. Hist. Survey, Champaign, Illinois.
- Turner, B.L. & S.D. Sundberg. 1986. Systematic study of *Osbertia* (Asteraceae-Astereae). *Pl. Syst. Evol.* 151:229-239.
- Zardini, E.M. 1978. Novedades en el género *Noticastrum* (Compositae - Astereae). *Hickenia* 1:134-138.

APPENDIX 1. Notes on character variation

1. The ancestral chromosome number for the *Heterotheca* lineage appears to be $x = 9$, based on the hypothesis that *Noticastrum* is closely related to *Osbertia* and *Chrysopsis* (Nesom 1991c), as well as on the taxa presumably most closely related to the goldenasters, including *Ionactis* and others (Nesom in prep.). The species of *Croptilon* have an aneuploid series of $n = 7$, $n = 6$, $n = 5$, and $n = 4$; the genus is scored with the $x = 9$ taxa, based on evidence presented by Smith (1966), who showed that the lower numbers within *Croptilon* are derived sequentially from the higher. Although no populations with $n = 8$ or $n = 9$ have been discovered, it is probable and assumed here that $n = 7$ in *Croptilon* has also been derived from a base of $x = 9$.

2. *Noticastrum* comprises both rhizomatous and taprooted species and it has been scored ambiguously. All species of *Heterotheca* are taprooted, except the rhizomatous *H. chihuahuana* (Turner & Sundberg) B. Turner and *C. mucronata* Harms ex Turner, which apparently are derived from taprooted ancestors. Plants of a previously undescribed species of *Ionactis* produce a taproot, but this is also apparently evolutionarily derived from the short, woody rhizomes of the other species (Nesom & Leary submitted).

3 and 4. *Pityopsis* and *Croptilon* stand alone among the other genera in their linear or narrowly oblong leaves with acute apices. The major foliar veins of *Pityopsis* are strictly parallel; the veins of *Croptilon* show a strong tendency to run parallel, usually with a single pair of laterals continuous from base to apex. And in contrast to the other genera, the foliar veins of both *Pityopsis* and *Croptilon* have large masses of associated sclerenchyma. Another distinctive feature of *Pityopsis* illustrated by Semple *et al.* (1980), the "sunken" abaxial epidermis, is present and even more pronounced in *Croptilon*, where it could be described as "lacunate."

5-9. Trichome terminology follows the designations in Nesom (1976), based on a study by Drury & Watson (1966). Type A trichomes have also referred to as "osteolate" (Semple *et al.* 1980) or as "helianthoid;" these are uniseriate and have thick, often roughened walls and the bases commonly are multicellular. Type B trichomes are also uniseriate but have thin, single celled bases and much thinner walls; in most taxa they are much smaller than the Type A trichomes, although in some of the goldenaster genera, they have supplanted the Type A trichomes and are the largest and most prominent. Type C trichomes are biseriate, usually with thin walled cells, and they typically are glandular in appearance. The simplest form has no head, with apical cells similar to the stalk cells - these are rarely found on herbage in the goldenaster group but elongated ones typically occur on the tubes of both ray and disc corollas. In the goldenasters, the apical cells are usually numerous and massed into a distinct, glandular head (3-8 cells wide at the apex) at the end of a stalk,

which is often long but variable in length among species. In these capitate trichomes, a droplet of transparent, yellow-orange resin may be formed at the tip of the head, and a membrane sometimes seems to enclose the droplet. Stages in the ontogeny of Type C trichomes have been documented and illustrated by Carlquist (1961).

Within *Noticastrum*, *N. hatschbachii* Zardini produces large glands; in the other species, Type C trichomes are present but unelaborated from the primitive biseriate, noncapitate form. Similar variation is present within *Heterotheca* sect. *Phyllotheca*. Various species within *Croptilon*, *Pityopsis*, and *Chrysopsis* usually lack Type C trichomes, but this is clearly a derived condition. In *Heterotheca* sect. *Ammodia*, there appear to be two distinct size classes of Type C trichomes, undifferentiated ones and large headed ones on thick stalks, although it is possible that these may simply represent ontogenetic stages.

In the tribe Astereae, Type A, B, and C or modifications of these appear to be the only kinds of trichomes present on the herbage. Homologies among trichome types can be established by examining the array of types present on a single plant. If only one of the uniseriate types is present, wall thickness and the nature of the trichome base are usually sufficient to distinguish it. The achene surfaces typically produce a second type of biseriate hair, the Zwillingshaare, which are ubiquitous throughout the tribe. Zwillingshaare rarely are produced on corollas, but they are primarily restricted to the achenes and have not been given an equivalent "Type" designation.

Type A trichomes are present in most species of all genera involved in the present analysis except *Pityopsis* and *Tomentaurum*, where they are completely absent. They are greatly reduced in number in *Croptilon*, where they are found primarily as spreading cilia along the petiolar margins. In *Osbertia*, *Chrysopsis*, and *Noticastrum*, Type A trichomes have thin, smooth, and vitreous walls, and they are commonly flattened and longitudinally twisted. In many taxa of *Chrysopsis* and *Noticastrum* they are distally elongated into fine, flexuous, flagelliform hairs. In the remainder of the goldenaster genera, the Type A trichomes are terete and have thicker walls. Semple et al. (1980) have shown that such trichomes in *Heterotheca* (including sects. *Heterotheca*, *Phyllotheca*, and *Ammodia*) have minutely papillate cell surfaces. Such surfaces apparently do not occur in other taxa of the goldenaster lineage, judging from studies with the compound microscope. *Heterotheca inuloides* Cass. produces vitreous trichomes similar to those in *Chrysopsis*, but they still have slightly papillate surfaces and certainly have developed their characteristics independently of those in the *Chrysopsis* lineage. In plants of *Heterotheca* the Type A trichomes often appear to be highly variable in length, even perhaps grading into Type B trichomes. Comparative data in greater detail (SEM) would be helpful for these taxa.

Type B trichomes are present in the goldenasters in their primitive form as thin walled, uniseriate hairs at least an order of magnitude smaller than

the Type A trichomes, except in the *Pityopsis* lineage, where they appear in several modifications. In *Pityopsis* and *Tomentaurum*, they are minutely and evenly filiform, forming a dense, close tomentum; they are parallel and sometimes anastomosing in *Pityopsis* but irregularly oriented and matted in *Tomentaurum*. In *Croptilon*, conspicuously lengthened Type B trichomes are apparent only on the abaxial surface of some species, where they originate in the "lacunae." On some plants of *C. divaricatum* (Nutt.) Rafn., these are dense enough to form a thin but conspicuous tomentum over the leaf surface. Some taxa of *Croptilon* and *Pityopsis* are glabrous or nearly so, lacking all trichomes.

10. Plants of *Tomentaurum* produce strictly monocephalous stems; those of *Osbertia* are mostly monocephalous, but the primary stems of *O. bartlettii* (S.F. Blake) Nesom produce a few lateral branches. Most species of *Noticastrum* are monocephalous, and *Heterotheca chihuahuana* is the only monocephalous species of its genus. It seems clear that monocephaly is a derived feature in the goldenasters, having arisen independently in several lineages.

11. The heads of *Croptilon* and *Pityopsis* are distinctly smaller than those of the other genera. Further, they are longer than wide, appearing cylindrical, in contrast to those in the rest of the goldenasters, which are about as long as wide. The heads of *Chrysopsis texana* (= *Bradburia*) are exceptionally small, but this certainly has resulted from the sterility of the disc flowers. Among the species of *Ionactis*, the heads of *I. cieloatica* are also small (Nesom & Leary submitted) and are reduced independently of the small ones among the goldenasters.

12. Keel'd phyllaries are one of the conspicuous features of the goldenaster group, although they are also characteristic of related genera (Nesom in prep.). At least on the basal portion of the phyllary, the medial nerve is indurated, not at all resinous, and sharply and narrowly raised. The medial nerve in phyllaries of *Croptilon*, and in some *Pityopsis*, is sometimes resinous from base to tip, lacking an indurated covering, but some taxa have a clearly discernible keel with a morphology that is similar to the other genera. The orange nerves in *Osbertia* also are sometimes exposed, and among the goldenasters, only its two species have completely herbaceous phyllaries without a distinct keel, although they are approached by some in *Chrysopsis*. The medial nerve in the phyllaries of *Noticastrum* is keel'd, but at least in the inner phyllaries there are usually an additional 1 or 2 pairs of smaller, unraised nerves conspicuously present on either side of the medial one.

13 and 14. In a phylogenetic overview of *Aster* and related groups (Nesom in prep.), the blue rayed genus *Ionactis* is the sister group of the yellow rayed genera of goldenasters. Ray color variation in *Noticastrum*, where white rays apparently are derived from yellow ones, is discussed in more detail in another paper (Nesom 1991c).

The primarily yellow rayed *Machaeranthera* alliance also appears to be

closely related the *Aster* group, based on molecular data of Suh (1989) and Morgan (1990). Only two genera within it have white or blue rayed taxa: *Machaeranthera* (sensu Hartman 1990), which comprises both yellow and white or blue rayed species, and *Xylorhiza*, where all taxa are white or blue rayed. Morgan's molecular data show *Xylorhiza* to be the most primitive genus in the *Machaeranthera* lineage, its position there analogous to that hypothesized for *Ionactis* in the goldenaster lineage. Both yellow and white rayed species are hypothesized to occur within the genus *Tonestus* A. Nels. (Nesom 1991d) as well as among genera related to *Gutierrezia* Lag. (Nesom in prep.).

15. The corollas of postreceptive ray flowers in most genera of the goldenaster lineage coil tightly inward, with the adaxial surface exposed. However, they remain straight in *Noticastrum* and *Osbertia*, as well as in two species of *Chrysopsis*, where that behavior is hypothesized to have arisen in parallel with the former two genera (Nesom 1991c). Coiling ray corollas occur in most of North American Astereae, including the *Aster* and the *Machaeranthera* lineages. Ray corollas in *Erigeron* L., however, display a number of different behaviors, although for the most part the behavior appears to be consistent among species of a single section (Nesom 1989). Further aspects of variation in ligule behavior in the family are noted by Stirton (1983).

16. The difference between sinuate and straight walls can be easily seen in the cells of the upper throat of the disc corollas. Sinuate walls are particularly characteristic of the disc corolla throats in some groups of *Aster* as well as related genera but not in the goldenasters.

17. Relatively large, elongate, straight sided crystals are found in the throat cells of all species of species of goldenaster except *Chrysopsis tezana*. Straight sided crystals much reduced in size occur in *C. pilosa*. The occurrence of these crystals appears to be one of the most significant diagnostic features of the goldenaster lineage, and their absence or reduction in two taxa clearly within the lineage on the basis of other characters is interpreted as apomorphic. The disc corolla tubes usually produce stellate "sand" crystals, and the transition between the large crystals of the throat and the much smaller "sand" crystals of the tube is abrupt. The disc corollas of *C. tezana* produce only "sand" crystals. Both species of *Osbertia* produce only straight sided crystals in the disc corollas, from the base of the tube into the throat.

In a survey of disc corolla morphology of other genera of American Astereae, crystals similar to those in the goldenasters have been observed (Nesom *et al.* submitted) only in the genus *Xylorhiza* (8 species examined), *Grindelia* (8 species examined), *Prionopsis* Nutt., and *Hazardia* E. Greene (4 species examined), where they are highly reduced in size. The following genera have been examined and found to produce only "sand" crystals (number of species studied in parenthesis, if more than one): *Aphanostephus* DC., *Aster* sensu lato (18), *Baccharis* L., *Boltonia* L'Herit., *Chaetopappa* DC., *Chloracantha* Nesom *et al.*, *Corethrogyne* DC., *Ericameria* Nutt., *Erigeron* (11), *Euthamia* Nutt.,

Gutierrezia, *Gymnosperma* Less., *Haplopappus* DC. (3 South American), *Hysterionica* Willd., *Isocoma* Nutt., *Machaeranthera* (8), *Monoptilon* Torr. & Gray, *Olivaea* Sch.-Bip. ex Benth., *Oonopsis* E. Greene (2), *Oritrophium* (Kunth) Cabr., *Petradoria* E. Greene, *Pyrrocoma* Hook., *Solidago* L. (3), *Stenotus* Nutt., *Stephanodoria* E. Greene, *Tonestus* A. Nels. (6), *Townsendia* Hook., *Vanceleva* E. Greene, *Xanthisma* DC., *Xanthocephalum* Willd. (5), and *Xylothamia* Nesom *et al.* In these genera, the crystals may be restricted to the corolla tube or they may extend into the throat.

18. The disc corolla lobes are either glabrous, invested with Type C trichomes noncapitate or only slightly capitate, or else they have uniseriate, acicular hairs clearly homologous with Type A trichomes found elsewhere on the plant. The occurrence of the latter on disc corolla lobes is rare in the Astereae (Nesom pers. obs.), and this feature probably has had a single origin in the goldenaster lineage, with losses in a number of the taxa; the distribution of character states could with equal parsimony be regarded as a number of parallel gains.

In *Pityopsis*, only *P. falcata* (Pursh) Nutt. and *P. ruthii* (Small) Small have disc corolla lobes with Type A trichomes. Lobes of the other species of *Pityopsis* usually have Type C trichomes or else they are glabrous, although some individuals of *P. microcephala* (Small) Semple produce Zwillingshaare on the disc corolla lobes. *Pityopsis falcata* and *P. ruthii* are among the four species hypothesized by Semple & Bowers (1985), apparently based on their geographic distribution, to be the most primitive in the genus. The genus is scored here as primitively possessing Type A trichomes on the disc corollas. Similar variation occurs in *Noticastrum*, where only *N. hatschbachii*, *N. acuminatum* (DC.) Cuatr., and *N. macrocephalum* (Baker) Cuatr. have lobes hairy with Type A trichomes.

19. The vascular traces, usually of 2-4 veins extending to nearly the tip of the style appendages, are densely sclerified in all of the goldenaster genera. Sclerification of such traces is variable in other genera of Astereae (Nesom pers. obs.).

20-24. Possible homologies among the different achene morphologies are among the most difficult to interpret. The achenes of *Noticastrum*, *Heterotheca* sect. *Ammodia*, *Tomentaurum*, *Pityopsis*, *Croptilon*, and *Osbertia* produce 6-26 thin, whitish, superficial and slightly raised, evenly spaced nerves; *C. rigidifolium* (Smith) Smith has four resinous, larger nerves interspersed between smaller ones. In cross section, the achenes are fusiform and terete to slightly compressed (in *Pityopsis*, *Osbertia*, and *Croptilon*), but among the goldenasters compressed achenes appear to be primitive. In *Heterotheca* sect. *Ammodia* and *Tomentaurum* the achenes are very strongly compressed; in *Noticastrum* they are plump but distinctly compressed. The ray achenes of *Heterotheca* sect. *Heterotheca* are 3 angled, most in sect. *Phyllotheca* are 2 angled, but those of *H. stenophylla* are slightly but distinctly 3 angled.

In *Heterotheca* sects. *Heterotheca* and *Phyllotheca*, one to several of the facial nerves of the disc achenes are resinous and clearly evident but not raised above the achenial surface. No other achenes of the group are like these, although three specialized species of *Chrysopsis* and one of *Croptilon* produce thick, distinctly raised, resinous veins. The achenes of most *Chrysopsis* (including *Bradburia*) are distinctive in their walls with broad and rounded ridges, the nerves completely below the surface. This feature separates *Chrysopsis* from *Osbertia* and *Noticastrum*, but it is not found in any of the other goldenaster genera. The achenes of *H. oregona*, with numerous superficial nerves, are most like those of *Tomentaurum*, although none of the goldenaster achenes have as many nerves (10-14) as in *H. oregona*. The 2-3(-6) nerved achenes of *Ionactis* are probably themselves evolutionarily derived from immediate ancestors with a greater number of achenial nerves, since these are common among the genera with keeled phyllaries and a base chromosome number of $x = 9$.

Among the taxa of *Heterotheca* sect. *Heterotheca*, achene shape is relatively constant. In *Heterotheca* sect. *Phyllotheca*, the achenes vary from long and nearly straight sided, much like *H. oregona*, to shorter and obovate as in sect. *Heterotheca*. The achenes of *Noticastrum*, while somewhat obovate, are relatively long.

25. In the goldenaster lineage, the pappus typically comprises numerous, basally terete, antrorsely barbellate bristles and an additional, very short, "outer" series of setae, very slender bristles, or linear scales. In *Osbertia* and *Croptilon* there is no outer pappus and the bristles are somewhat reduced in number; in some species of *Chrysopsis* as well as in *Heterotheca* sect. *Ammodia*, the outer pappus is represented only by a few inconspicuous setae. Both *Chrysopsis* and sect. *Ammodia* have been scored as having an outer pappus, and in the phylogenetic hypothesis presented here, its apparent total absence in the other two genera is interpreted as apomorphic. A double pappus also occurs in *Ionactis* and apparently is primitive for the goldenasters as well as related groups (Nesom in prep.).

26. The pappus bristles in most of the goldenasters are terete from base to tip, with the divergent, "ciliate" hairs emerging spirally from all around the bristle. In contrast, the bristles of *Heterotheca* can be seen to be flattened, with the cilia arranged in two lateral rows, even though they are very slender. In some cases, this is most apparent immediately above the bristle base. There is variation among the species of *Ionactis*, but it has been scored as having terete bristles (see comments in Nesom & Leary submitted).